

Team 359

PROBLEM B: DINOSAURS VERSUS MAMMALS

November 13, 2016

We study the behavior of two models (Power Law and Gompertz) for the evolution of the maximum body mass of mammals and we apply the best of these two models to the available data of the maximum body mass of dinosaurs over time. Using the model for dinosaurs we found no relation between atmospheric oxygen levels and maximum body size over time before the K/Pg event. We also found the evolution of maximum ground rates versus body temperatures for both mammals and dinosaurs. Finally, we provide the entire evolution of atmospheric oxygen levels and the entire evolution of the maximum body size before and after the K/Pg event.

INTRODUCTION

One of the most recognizable characteristic of dinosaurs is their size, and even though they came in a great variety of sizes, larger dinosaurs tend to be more captivating. This might result from the fact that at the present time we don't see around creatures with the dimensions that dinosaurs had, which were up to 40 m long, 20 m tall, and 70 tons of weight [1]. Today, the largest living (terrestrial) animals are mammals, and the largest mammal is the African Elephant (*loxodonta* genus), which reaches an average mass of 5 tons [2]. This huge disparity in masses could be erroneously explained from the conception that mammals haven't had the time that dinosaurs had for expanding their sizes, since now we know that the first modern mammals (not therapsids) appeared about 225 Ma ago [3], whilst dinosaurs appeared about 230 Ma ago [4]. However, it is true that besides the fact that dinosaurs and mammals shared the same time and place, mammals were very small compared to present day mammals. In this sense, the triggering event for mammal evolution was the extinction of dinosaurs, which opened new niche spaces that were used with evolutionary opportunism. Non-avian dinosaurs extinction (along other species extinction) was caused by the Cretaceous/Paleogene (K/Pg) event that occurred approximately 66 million years ago [5]. However, despite the lack of predators, mammals did not get as massive as dinosaurs got. In this work we study the behavior of two models for the evolution of the maximum body mass of mammals and then we apply this models to the available data of the maximum body mass of sauropoda over time, and contrast the information from both models and from both species. We choose sauropoda over other dinosaurs since they were the largest dinosaurs before the K/Pg event according to fossil data [9].

EVOLUTION OF MAXIMUM BODY SIZE MODELS

We started with the models provided by Felisa A. Smith et al, which are a simple growth model featuring a power law function and a sigmoidal growth model. The simple growth model predicts an unbounded increase in the maximum body size (M) as the following power law

$$\log(M) = M_0 t^\gamma$$

where t is time, M_0 is the initial maximum body size and γ takes the value of $1/2$ since the model is based on a diffusive evolution where body size is equally probable to increase or decrease. Nevertheless, in this type of evolution, the maximum of a trait (in this case the maximum body size) increases with the square root of time [7].

The previous model is contrasted with a model that, unlike the previous, takes into account the upper limits in body sizes provided by unavoidable restrictions, for instance, physiological and allometric constraints, or by the fact that we have a finite amount of resources. This set of constraints is added into the model as an asymptotic body mass constant K . Then, the model describes the rate of change in body mass with respect to time $\frac{dM}{dt}$ as a function of the mass at a given time which approximately increases at a some constant rate (α), and, on the other hand, this rate of change in mass is diminished by the difference between the asymptotic mass K and the mass at a given time t .

$$\frac{dM}{dt} = \alpha M (\log(K) - \log(M))$$

$$\frac{dM}{dt} = \alpha M \log\left(\frac{K}{M}\right) \quad (1)$$

Then the solution to the previous differential equation is given by

$$\log(M) = \log(K) - \log\left(\frac{K}{M_0}\right) e^{-\alpha t} \quad (2)$$

where M_0 is the initial maximum body size. Notice that equation (2) is a Gompertz function, which is characterized by a slow growth α at the start and at the end of the time period (a sigmoidal type of behavior).

We gathered the data of the maximum body size of mammals and sauropoda at different periods of time, and then for both models we used a least squares fitting technique in order to find the best possible fits.

A. Maximum body size evolution in Mammals

A.1. Power Law model

Using the maximum body sizes over time of different lineages (such as pantodonta which is now extinct, and proboscidea, the lineage of modern elephants) reported in [8] we found the following fit in the case of the Power Law model.

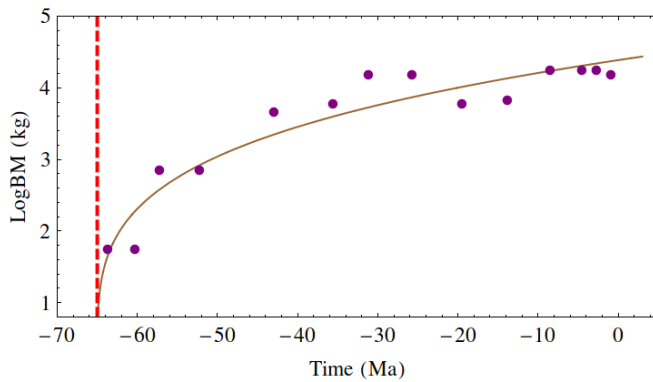


Fig. 1. Best fit curve for the maximum body mass evolution of ordinary mammals using the Power Law model.

The γ parameter of our curve was smaller than the predicted value of $1/2$ [7], and than the previously reported value of $1/4$ [8]. We found $M_0 = 1.582$ and $\gamma = 0.243$. Therefore our fit adjusts better to the body size peak in largest mammals between -50 Ma and -20 Ma.

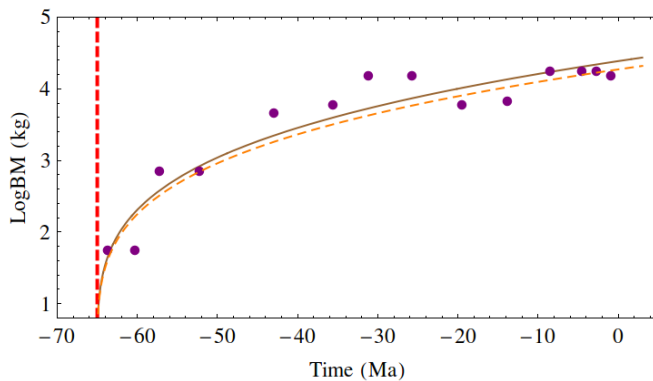


Fig. 2. Comparison between our fit to the data vs Felisa A. Smith et al. [8] fit for ordinary mammals using the power law model, dashed lines shows the best fit reported in [8].

A.2. Gompertz Model

This model reproduces the upper limit in body mass inherent to any lineage. Thus, it is a better model than the previous one.

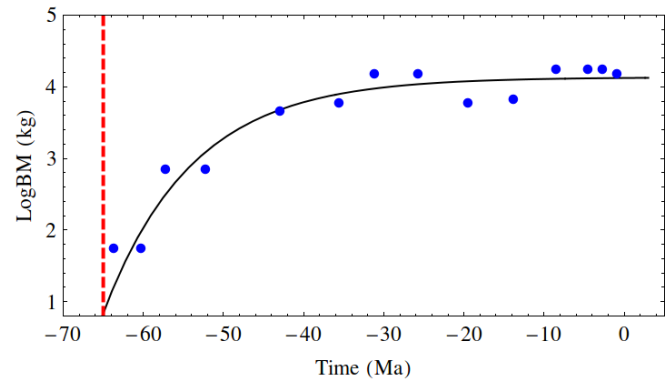


Fig. 3. Best fit curve for the maximum body mass evolution of ordinary mammals using the Gompertz model.

As with the previous model, in the Gompertz model we also found a difference between our fit and the one reported. The curve we found adjusts better to aforementioned peak in maximal body size.

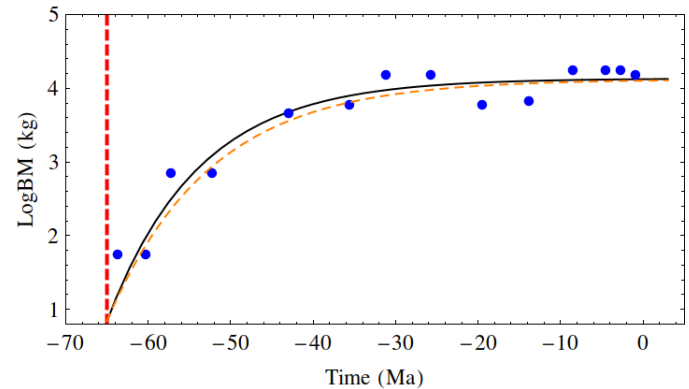


Fig. 4. Comparison between our fit to the data vs Felisa A. Smith et al. [8] fit for ordinary mammals using the Gompertz model, dashed lines shows the best fit reported in [8].

B. Maximum body size evolution in Sauropoda

The Sauropoda masses (Table 1) over time were taken from the mass estimates presented by Benson RBJ et al. (2014), where they use a large set of fossil data (for instance femur length and/or circumference) in order to predict the body mass [6].

Table 1. Sauropod masses [6]

Mass (Kg)	Age (Ma)
2,000	220
10,000	200
5,600	198
7,400	185
4,500	168
30,000	160
75,000	150
65,000	147
15,000	130
25,000	120
70,000	95
65,000	80
60,000	65

With the previous data on hand we were able to make the same analysis that was made for mammals, i.e. we found the best fit curve for both, the power law model and the Gompertz Model:

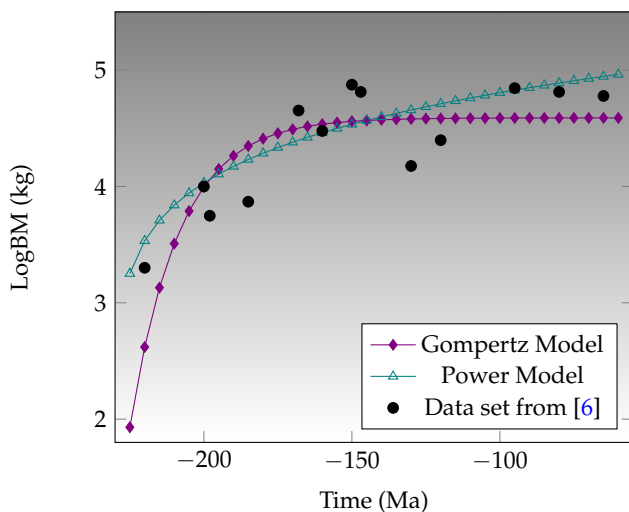


Fig. 5. Evolution of the mass of sauropod using both models presented with the data given in Benson RBJ et al. [9]

As we can see, the Gompertz model adjusts better to the plateau due to the upper limit in body mass size imposed by allometric or biomechanical constraints.

C. Atmospheric Oxygen Analysis

We gathered information of the atmospheric oxygen levels before the K/Pg event and we found no relation between the changes in the atmospheric levels of oxygen and the change in the maximum body mass of sauropoda, here we present both changes in the same period of time from -220 Ma to -65 Ma.

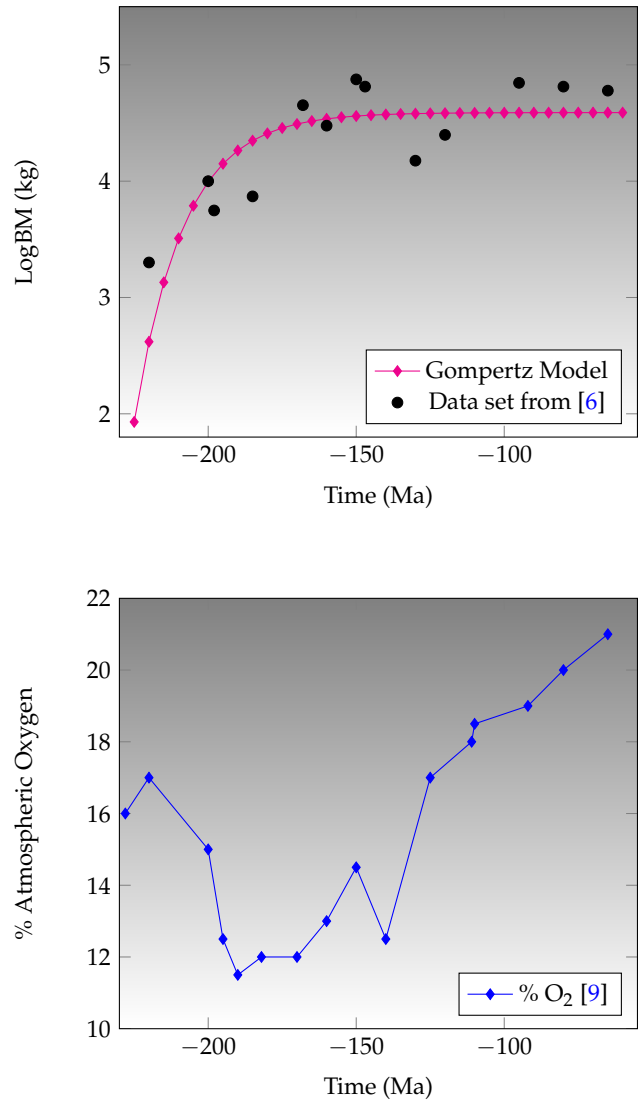


Fig. 6. Evolution of the mass of sauropod (upper figure) and comparison with the evolution of percentage of atmospheric oxygen level (lower) in the same period of time.

The evolution of the maximum body mass of the sauropoda reaches a plateau around 170 Ma, whilst the level of oxygen fluctuates before it reaches a maximum peak near the K/Pg event.

D. Body temperature and maximum growth rate (MGR)

We consider the evolution of the growth rate of sauropoda and elephants with respect to their body temperature. It was pointed by [10] that body temperature adaptations were crucial for the development of body size in dinosaurs. The high growth rates could indicate a higher level of metabolism, this would require a greater surface area since more heat must be dissipated from the body.

Furthermore, Gillooly et al.[11] established a link between the body temperature and the maximum growth rate in which the individual growth rate is given by:

$$T_b = 10 \ln \left(\frac{MGR \times M^{-3/4}}{g_0} \right) \tag{3}$$

where the parameter $g_0 \sim 2 \times 10^{-4} \text{ kg}^{1/4} \text{ day}^{-1}$, M is the mass of the species and MGR the maximum growth rate. We are setting an average mass $M = 50000$ for sauropod and $M = 5000$ for the elephant.

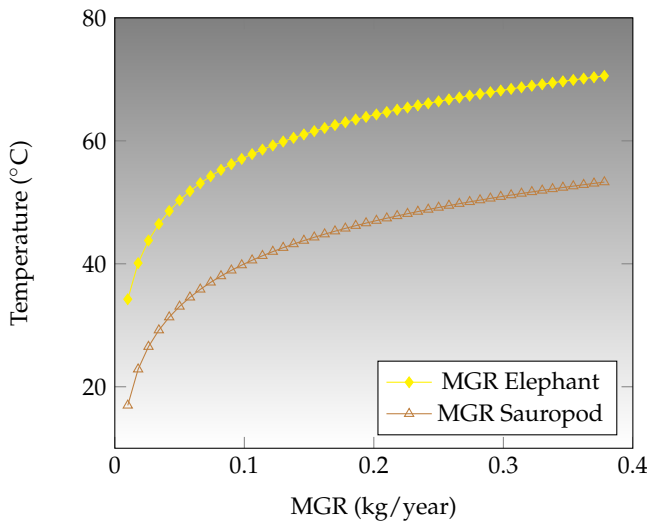


Fig. 7. Comparison MGR (maximum growth rate) between a sauropod and an elephant for body temperature T_b .

We found, as expected, that the elephant needs a lower MGR in order to adapt itself to ambient temperatures.

1. CONCLUSION

We first analyzed the result given by [8] only for mammals and found a difference in the parameters, we did so by using the least square fitting method shown in Appendix A. Then we developed a Mathematica code in order to compare the Power law and Gompertz model. In the following plot we present the curves given by both models, using our results and comparing them with those given by [8](dashed curves).

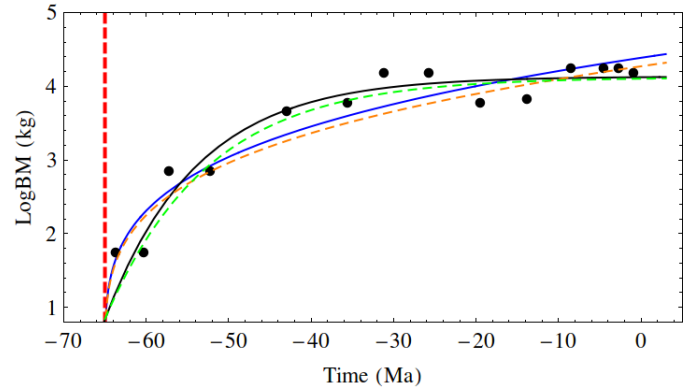


Fig. 8. Maximum mass evolution of mass using both models. Our curves are the continuum lines. Those given by Felisa A. Smith et al., are the dashed lines [8].

As we can see the Gompertz method was able to reproduce the plateau behavior due to biological constraints of mammals.

Once we applied the Gompertz method to the available data for sauropoda, we found the parameters that best adjusted the curve to the given data (see Appendix A). And with the adjusted model we saw no relation between the atmospheric oxygen levels and the maximum body size of sauropoda. In Appendix B we present the errors in both models.

Finally, we present (Figures 9 and 10) the entire evolution of atmospheric oxygen levels(Figure 9), and the entire evolution of the maximum body size before and after the K/Pg event.

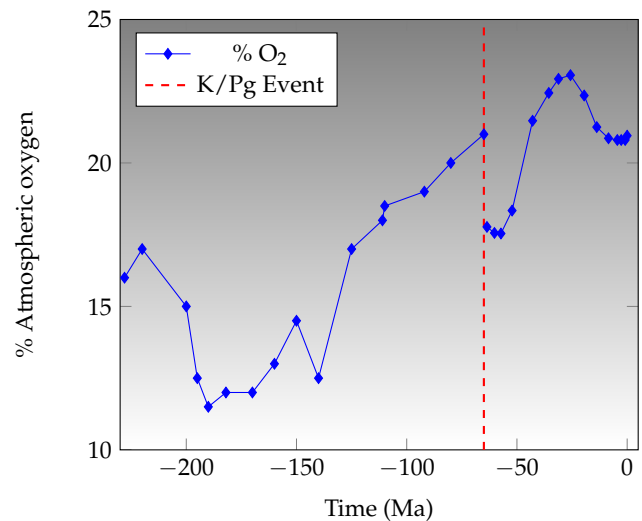


Fig. 9. Evolution of the % of atmospheric oxygen on Earth.

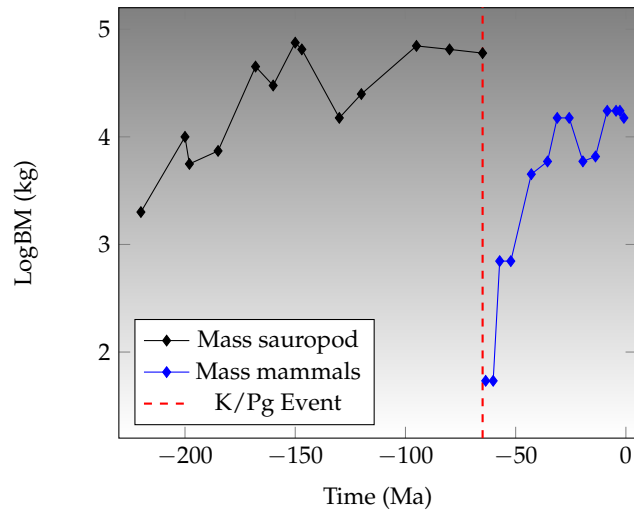


Fig. 10. Evolution of the mass of sauropod (??) and ordinary mammals.

REFERENCES

1. J. M.; Martínez, R. N. (2015). "Bone Cells in Birds Show Exceptional Surface Area, a Characteristic Tracing Back to Saurischian Dinosaurs of the Late Triassic". *PLoS ONE*. 10 (4): e0119083.
2. Laurson, Barry; Bekoff, Marc (1978). "Loxodonta africana" (PDF). *Mammalian Species*. 92: 1–8. doi:10.2307/3503889. Retrieved 5 August 2010.
3. Hunt, David M.; Hankins, Mark W.; Collin, Shaun P.; Marshall, N. J. *Evolution of Visual and Non-visual Pigments*. London: Springer. p. 73. ISBN 978-1-4614-4354-4. OCLC 892735337.
4. Alcobar, Oscar A.; Martinez, Ricardo N. (19 October 2010). "A new herrerasaurid (Dinosauria, Saurischia) from the Upper Triassic Ischigualasto Formation of northwestern Argentina". *ZooKeys*. 63 (63): 55–81. doi:10.3897/zookeys.63.550. PMC 3088398. PMID 21594020.
5. Renne, Paul R.; Deino, Alan L.; Hilgen, Frederik J.; Kuiper, Klaudia F.; Mark, Darren F.; Mitchell, William S.; Morgan, Leah E.; Mundil, Roland; Smit, Jan (7 February 2013). "Time Scales of Critical Events Around the Cretaceous-Paleogene Boundary". *Science*. 339 (6120): 684–687. Bibcode:2013Sci...339..684R. doi:10.1126/science.1230492. PMID 23393261.
6. P. M. Sander et al., *Biology of the sauropod dinosaurs: the evolution of gigantism*, *Biol. Rev.* (2011), (86), pp. 117-155.
7. Trammer J., *Maximum body size in a radiating clade as a function of time*, *Evolution*, 59(5), 2005, pp. 941–947.
8. Felisa A. Smith et al., *The Evolution of Maximum body size of terrestrial mammals*, *Science* (2010) **6008**, pp. 1216-1219.
9. Benson RBJ et al. (2014) Rates of Dinosaur Body Mass Evolution Indicate 170 Million Years of Sustained Ecological Innovation on the Avian Stem Lineage. *PLoS Biol* **12**(5): e1001853. doi:10.1371/journal.pbio.1001853.
10. Griebeler EM, *Body temperatures in dinosaurs: what can growth curves tell us?*, *PLoS One* (2013) doi: 10.1371/journal.pone.0074317. eCollection 2013.
11. Gillooly JF, Alleen AP, Charnov EL (2006) Dinosaur fossils predict body temperatures. *PLOS Biol* 4: 1467-1469.
12. *Mathematica* 9.

APPENDIX A

Mathematica code with comments

Constants:

Felisa A. Smith et al.

*(*Gompertz model*)*

k=13,182.57

m0=6.92

 $\alpha=0.08$ *(*Power Law*)*

c0=1.504

 $\gamma=0.25$

Our constants:

*(*Gompertz model*)*

kk=13,547.17

M0=6.92

 $\beta=0.09$ *(*Power Law*)*

a0=1.5826

 $\zeta=0.2433$ *(* Supporting online material from Felisa A. Smith et al. *)*

```
A = List[{105.5, 5}, {70.6, 3.3}, {63.6, 54}, {60.2, 54}, {57.25,
700}, {52.2, 700}, {42.9, 4500}, {35.55, 5907}, {31.15,
15000}, {25.715, 15000}, {19.5, 5917}, {13.79, 6568}, {8.47,
17450}, {4.465, 17450}, {2.703, 17450}, {0.9035, 15000}, {0.013,
10000}];
```

```
A1 = Sort[Table[{Abs[A[[j,1]]-110], A[[j,2]]}, {j,1,17}]];
A2 = Sort[Table[{Abs[A[[j,1]]-65], N[Log[10,A[[j,2]]]]}, {j,3,16}]];

```

(Power Method *)*

```
H[t_] := a0*t^ $\zeta$ ;
```

```
 $\Pi$  = Expand[Sum[(H[A2[[j,1]]]-N[A2[[j,2]],20])^2, {j,1,14}]];

```

```
Minimize[ $\Pi$ , {a0,  $\zeta$ }, WorkingPrecision->20];

```

```
 $\Pi$ 1 = Expand[Sum[(H[A2[[j,1]]]-N[A2[[j,2]],20])^2, {j,1,14}]] /.  $\zeta$ ->1/4;

```

*(*Best fit curve with our constants*)*

```
Show[Plot[H[t], {t,0,65}, PlotStyle->{Red,Dashed}, AspectRatio->1],

```

```
ListPlot[A2,PlotStyle->{PointSize->.02,Black},

```

```
AspectRatio->1], Plot[c0 t^ $\gamma$ , {t,-5,75}]];

```

(Gompertz Model *)*

```
A3 = Sort[Table[{Abs[A[[j,1]]-65], N[Log[10,A[[j,2]]]]}, {j,3,16}]];

```

```
L[t_] := Log[10,kk]-Log[10,kk/M0]*Exp[- $\beta$ t];

```

```
 $\Gamma$  = Expand[Sum[(L[A3[[j,1]]]-N[A3[[j,2]],20])^2, {j,1,14}]] /. M0->6.92;

```

```
FindMinimum[ $\Gamma$ , { $\beta$ ,  $\kappa$ }, MaxIterations->1000, WorkingPrecision->1000];

```


(* Best fit curve with our constants for the Gompertz Model *)

```
Show[Plot[L[t], {t,-5,65}, PlotStyle->Green, AspectRatio->1,
PlotRange->{{-10,67}, {0,5}},
Plot[Log[10,k]-Log[10, k/m0]*Exp[-αt], {t,0,65},
PlotStyle->Pink]];
```

(* Generating our best fit function for Sauropod masses using Gompertz Model*)

Table 1

```
MM = List[{220, 2000}, {200, 10000}, {198, 5600}, {185, 7400}, {168,
45000}, {160, 30000}, {150, 75000}, {147, 65000}, {130,
15000}, {120, 25000}, {95, 70000}, {80, 65000}, {65, 60000}];
```

```
M1 = Table[{Abs[MM[[j,1]]-230], N[Log[10, MM[[j,2]]],5]}, {j ,1,13}];
```

```
ListPlot[M1,Joined->True, Mesh->All, PlotStyle->{PointSize ->.015, Blue}, AspectRatio->1/2,
PlotRange->{{0,230}, {0,5}}];
```

Do[

```
  K = Expand[Sum[(P[M1[[j, 1]]] - N[M1[[j, 2]], 20])^2, {j, 1, 13}]] /.mm0 -> j;
  Sol = FindMinimum[K, {δ, ν},
  MaxIterations->1000, WorkingPrecision->100]; Eg = Sol[[1]];
  If[Eg < Mini, Mini = Eg; DatoMi = {Sol[[1]], {δ, ν, j} /. Sol [[2]]}];
  Print[j, "", N[Eg, 10], "", N[Mini, 10], {j, 1, 10, .1}
```

];

(* Our best fit function for the mass of Sauropod *)

```
Show[Plot[P[t], {t ,10,180}, PlotStyle->Black, PlotRange->{{0,180}, {1.5,5}},
ListPlot[M1, PlotStyle->{PointSize->.015, Blue},
AspectRatio->1/2, PlotRange->{{0, 230}, {0, 5}},
ListPlot [{12, Log[10,7500]}],
PlotStyle->{PointSize->.015, Blue}]]
```

(* Calculating the best fit function for the mass of Sauropod using power method *)

```
MM1 = List[{220, 2000}, {200, 10000}, {198, 5600}, {185,
7400}, {168, 45000}, {160, 30000}, {150, 75000}, {147,
65000}, {130, 15000}, {120, 25000}, {95, 70000}, {80, 65000}, {65, 60000}];
```

```
M2 = Table[{Abs[MM1[[j,1]]-230], N[Log[10,MM1[[j,2]]], 5]}, {j,1, 14}];
```

```
H1[t_] := a1*t^ξ1;
```

```
Π0 = Expand[Sum[(H1[M2[[j,1]]]-N[M2[[j,2]], 20])^2, {j, 1, 14}]];
```

```
Minimize[Π0, {a1, ξ1}, WorkingPrecision->20];
```

```
Π0 = Expand[Sum[(H1[M1[[j,1]]]-N[M1[[j,2]], 20])^2, {j, 1,13}]] /. a1->2.5;
```

```
FindMinimum[Π0, {a1, ξ1}, WorkingPrecision->200];
```

(* Our best fit function for the mass of Sauropod using power method *)

```
Show[Plot[H1[t], {t ,5,190}, PlotStyle -> {Red, Dashed},
PlotRange->{{0, 190}, {3,5}},
ListPlot[M2, PlotStyle->{PointSize->.015, Blue},
AspectRatio->1/2, PlotRange->{{0,230}, {0,5}}]]
```

APPENDIX B

Error estimation for both models

Here we provide the tables of deviations for each model at distinct times, in the case of mammals we start from present day to the K/Pg event, and for sauropoda we start at the K/Pg event and go backwards in time up to -220 Ma.

Time (Ma)	LogBM (kg)	% (Error) P. L.	% (Error) G.
0.9035	4.17609	4.45234	1.32413
2.703	4.2418	2.25566	2.96346
4.465	4.2418	1.55203	3.01542
8.47	4.2418	0.14716	3.16948
13.79	3.81743	7.61714	6.86929
19.5	3.7721	5.9759	7.47792
25.715	4.17609	7.98712	3.47411
31.15	4.17609	12.0828	5.04933
35.55	3.77137	4.806	3.28225
42.9	3.65321	9.07759	0.76539
52.2	2.8451	2.62367	7.97356
57.25	2.8451	10.3902	14.119
60.2	1.73239	24.2304	13.1544
63.6	1.73239	3.10347	40.8693

Table 2. Mammals

Time (Ma)	LogBM (kg)	% (Error) P. L.	% (Error) G.
65	4.7782	3.3889	4.11458
80	4.8129	1.56664	4.87805
95	4.8451	0.352391	5.59426
120	4.3979	6.64289	4.07181
130	4.1761	10.3325	8.83096
147	4.8129	5.67783	5.43477
150	4.8751	7.51634	6.91019
160	4.4771	0.334964	1.29092
168	4.6532	5.81107	3.34703
185	3.8692	8.56669	11.0167
198	3.7482	7.72829	7.75404
200	4.0000	0.763681	0.0961012
220	3.3010	6.56391	26.0156

Table 3. Sauropoda